INTRODUCTION

The aquaculture industry has been growing globally over the past few years due to the increasing demand of protein consumption by human population worldwide, and fish are the most farmed animals in this animal production system. Under farm conditions, the environments where fish are kept have been frequently arranged based just on economic and ergonomic requirements, thereby neglecting considerations related to fish welfare. Moreover, it is evident that, whilst fish farming is of fundamental importance for the animal production system on a worldwide scale, these animals are commonly exposed to poor and unfavourable conditions under farm systems that can severely impair their welfare state and the quality of the final product for the farmers. Several farm procedures, including fish handling processes, pre-slaughter and slaughter, may also evoke a strong stress response in fish,1 with an important negative effect both on fish welfare and on the quality of fish flesh.2,3 This is worsened by the low level of domestication of many widely-farmed fish species,4 as such species can be more severely affected in captivity.5 On the other hand, there is an increasing awareness amongst the public (and thus amongst the potential consumers), about the importance of taking the welfare conditions of fish into account.6 A recent survey within the European Union showed that consumers are becoming more demanding in relation to the conditions in which

Environmental enrichment in fish aquaculture: A review of fundamental and practical aspects

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Environmental enrichment (EE) can improve the welfare of captive fish. Its objective is to provide new sensorial and motor stimulation in order to help meet their behavioural, physiological, morphological and psychological needs, whilst reducing stress and frequency of abnormal behaviours. In fish farms, rearing environments are usually designed from a human perspective and based on economic requirements, mainly for practical reasons for the farmer, with little consideration for animal welfare. Throughout aquaculture production cycles, many farming operations can be stressful for fish, and EE may not only help them cope with these stressful events but also improve their overall welfare. In recent years, increasing interest on the effects of EE in captive fish has focussed mainly on structural enrichment. However, there are many other enrichment strategies that merit attention (e.g. sensorial, occupational, social and dietary enrichment) and which may be of interest for fish farming. Here, we review in depth the existing literature on EE and its effects on the welfare of a wide range of farmed fish species, discussing the feasibility and potential applications of different EE strategies to promote fish welfare at a commercial scale. We also present a practical framework to address the design, validation and implementation of EE by the aquaculture industry, taking in consideration the technical challenges of providing enrichment for farmed fish.

KEYWORDS
aquaculture, environmental enrichment, fish welfare, management, positive stimulus, stress response
fish are farmed. This, coupled with the idea that better welfare conditions also help to improve the product quality and potentially the profitability, opens the door to the use of environmental enrichment (EE) techniques to improve the quality of life for fish in farms by giving them the opportunity to experience positive aspects in their environment. In this sense, EE in aquaculture can be understood as providing new environmental stimuli (motor or sensor stimulation) to help captive fish to meet with their physiological, behavioural and psychological needs. This EE definition encompasses the three main aspects defining animal welfare in terms of proper biological functioning: functional, natural and feeling-based. In fact, the Council of Europe Directive 98/58/EC of 20 July 1998, concerning the protection of animals kept for farming purposes (which includes fish), states that the biological characteristics and different species-specific needs of the fishes should be taken into account in husbandry practices, especially “with respect to the requirements for water conditions, social behaviour and environmental structures”. In order to avoid detrimental effects on fish welfare, it is important to consider how biological characteristics interact with farming systems using both scientific and practical knowledge, and how EE can be successfully applied in fish culture conditions.

The benefits of using EE on land-farm animal welfare and productivity have been widely demonstrated, but the EE needs of aquatic farmed animals have been largely overlooked. The neglect of aquatic EE is mostly due to the debate on whether fish are sentient and capable of suffering (which now is clear), as well as to the difficulty of observing aquatic animal behaviour in farming settings. In addition to this, there is the specificity of EE needs in the wide range of farmed aquatic species, which comprise very diverse taxonomic groups, contrary to land-farmed animals. At this point, it is relevant to consider that giving positive stimuli to fish, which can elicit some positive feelings, is as important as the need to prevent or minimise fish suffering under captive conditions. Accordingly, the reformulated proposal of the ‘five domains’—nutrition, environment, health, behaviour and affective experiences—which should be considered to properly evaluate the welfare state of an animal, also addresses the positive aspects of welfare instead of focussing just on the negative ones. For example, when considering the behaviour domain, not only the restrictions of behavioural expressions should be taken into account, but also if the animal has the possibility to express rewarding behaviours (e.g. environment-focussed exploration, food acquisition activities, animal-to-animal interactive activities), all of which can generate various forms of comfort, pleasure, interest, confidence and a sense of control. The same should be regarded for all the other welfare domains. This is also in agreement with the concept of quality of life, which addresses the overall balance between negative and positive experiences at a particular period of the animal’s life. Thus, a ‘life worth living’ (as proposed by UK Farm Animal Welfare Council) is reached when positive events predominate in this balance over the whole life of the animal. A good way to improve such positive experiences for fish, as for other animals, is to properly implement techniques of EE.

Because of the variety of EE that can be provided, as well as the wide range of species that can benefit from it, EE science is constantly improving. Even though there is extensive information about the effects of EE on fish welfare concerning physiology and behaviour of laboratory (e.g. zebrafish, three-spined stickleback) and ornamental fish (e.g. guppies, goldfish), this review focuses only on fish species of aquaculture interest. Unlike other sectors with captive fish (laboratory and ornamental fish), aquaculture produces fish for human consumption, and therefore, aspects related not only to ethical issues (e.g. welfare) but also reputation and production efficiency (e.g. growth performance, feasibility, certifications) are essential. In this sense, there are some very comprehensive reviews on physical enrichment or specific colour preferences in cultured fish, but there is no work to date that encompasses all five recognised categories of EE (physical, sensorial, occupational, social and dietary enrichments). Therefore, the main goal of the recent review is expanding the over-the-horizon views on different strategies and alternatives for enriching the fish environment in world-wide aquaculture, compiling the existing knowledge on the effects on fish welfare, assessing possible benefits for the industry or applications at industrial scale and providing guidelines for fish-farmers, researchers and other stakeholders.

To fulfil the aim for this review, relevant peer-reviewed literature were sought for using Google Scholar and Web of Science databases. We retrieved articles based on their relevance to the search strings including fish species of aquaculture interest and the five enrichment strategies, as well as the different methodologies that could be used within each enrichment strategy. Additional articles and technical reports provided by experts in the field were also included. In addition, articles were checked for relevance and grouped into general categories (EE strategies) for discussion, comprising research foci on fundamentals and discussing feasibility and further steps of EE in aquaculture.

### 2 | ENVIRONMENTAL ENRICHMENT STRATEGIES

#### 2.1 | Physical enrichment

Physical enrichment consists of adding physical complexity with structures, objects or any structural modification to increase heterogeneity of the rearing environment. Some species use substrate or shelters in their natural environment, and, therefore, may also make frequent use of physical enrichment when in captivity. Such enrichment strategy can be created with a wide variety of features in many shapes and sizes, and they can be classified into two main types: (1) structures, which can provide shelter or simply add heterogeneity and complexity to the rearing environment; and (2) substrates, which are more appropriate for bottom-dwelling or bottom-user species, during their whole life or at specific life-stages (e.g. incubation). Structural enrichment is probably the best-known EE strategy and, therefore, the most used from laboratories to farms nowadays.
Physical enrichment for captive fishes has been addressed in depth by several recent reviews,22-24 which highlight the growing interest in this type of enrichment as well as the extent of its effects on fish welfare. We nonetheless include an overview here for the sake of completeness, with some additional studies and a focus on relevance to aquaculture for food production.

2.1.1 Structures

There is a wide range of studies on different fish species regarding physical EE that provided shelter in captivity. For instance, some work on catfishes (i.e. Clarias gariepinus, Heterobranchus longifilis, Silurus glanis, S. asotus) demonstrated that simple structures in the rearing environment, such as plastic strips, shreiddings, or tubes, can provide hiding places, inhibit cannibalism and aggressive behaviours and increase growth and survival (e.g. 26-30). A study on mangrove red snapper (Lutjanus argentimaculatus) showed that juveniles grow faster when provided with hard, complex structures, such as rock piles and mangrove roots.31 Similarly, studies on different salmonids showed that EE structures, such as plastic tubes and shredding, not only can improve growth and survival, but also swimming agility and physiological stress response (e.g. reduced plasma cortisol levels) when presented with stressors (e.g. air exposure, handling, crowding), as well as decreased fin damage and related fin infections (e.g. 23,32-34).

Indeed, studies on the Atlantic salmon (Salmo salar) demonstrated that adding complexity in the rearing environment not only promotes cognitive abilities and improves brain plasticity,35,36 but also decreases parasite occurrence and improves infection resistance and survival.37,38 Rearing Atlantic cod (Gadus morhua) in physically enriched environments that provide hiding places improves their learning capabilities and increases resting behaviour, thus affecting swimming activity and shoaling behaviour in the tank.39-42 In this sense, the level or intensity of physical structures (i.e. number of structures) reduces aggression and increases social stability of territorial species, such as black rockfish (Sebastes schlegeri) and fat greenling (Hexagrammos otakii).43 Similarly, the number of plastic plants provided as structural enrichment has direct effects on territoriality of cichlids, such as Nile tilapia (Oreochromis niloticus), redbreast tilapia (Tilapia rendelli) and convict cichlid (Amatitlania nigrofasciata), and reduces aggression.44-46

Recent studies have combined different types and levels of physical structures and plastic plants on larval and juvenile black rockfish.47-51 These studies indicated that enrichment levels have significant positive effects on growth performance, behaviour (especially aggression), brain plasticity and neurogenesis, physiological condition and stress-related physiological responses. The authors suggested that providing a medium-amount (approximately 50% basal-area coverage) of structural enrichment might be optimal for enhancing welfare and behavioural flexibility in the aquaculture industry. However, changes in behavioural responses to structural enrichment depend on ontogenetic life-stages of reared fish.52 Furthermore, Saraiva and Pompeu53 demonstrated that structural EE (submerged logs and artificial aquatic plants) can induce morphological differentiation in two Neotropical species (Prochilodus lineatus, Brycon orbignyanus) through phenotypic plasticity, potentially generating phenotypes more adapted to exploiting a complex environment. In addition, the use of nets in hatchery and nursery tanks is known to be widely used in gilthead seabream (Sparus aurata) and European seabass (Dicentrarchus labrax) farms (Arechavala-Lopez P. pers. obs.), with the aim of disrupting their circular swimming pattern when shoaling, thereby reducing vertebral malformations, although this has not yet been empirically tested. It is also known that some aquaculture companies use submerged rings that release curtains of air bubbles inside the net- pen (Sea Pen Aeration systems; KAESER ®, https://www.kaeser.com/int-en/solutions/aquaculture/), which increase the oxygen saturation of the water, thus lowering the feed conversion ratio, as well as preventing algae and plankton (including planktonic stages of sea lice Lepeophtheirus salmonis) from entering the sea cage, and improving the overall health of the fish (Kadri, S. pers. com.).

In this context, even if structural enrichment does not provide shelter, it can simply add environmental complexity and heterogeneity that can also improve the welfare conditions of captive fish. For example, adding vertically-suspended structures can modify the water flow and velocity profiles in fish tanks,54,55 and it has been demonstrated that substantial benefits can be accrued during rearing of four salmonid species. Jones et al.56 demonstrated that feed conversion rate can be improved in Atlantic salmon by inserting an array of suspended plastic conduits in the rearing tank, but did not report significant differences in individual fish length, total weight gain, individual weight or condition factor. White et al.57 conducted a similar study on brown trout (Salmo trutta) and rainbow trout (Oncorhynchus mykiss) and reported that total tank weight gain and feed conversion ratio can be significantly improved for both species reared with suspended conduit as enrichment. Other studies on rainbow trout tested different designs and densities of vertically-suspended structures (e.g. aluminium rods, aluminium angles, strings of coloured balls) in circular rearing tanks and reported benefits in total tank weight gain, feed conversion ratio and individual performance in the structurally complex tanks, with minimal effects on regular tank cleaning.58-64 Rosburg et al.65 showed that rearing chinook salmon (Oncorhynchus tshawytscha) in tanks with vertically-suspended arrays of polyvinyl chloride pipes or six golf balls fixed vertically on threaded rods can improve fish length, weight-gain and fin condition. Similarly, Voorhees et al.66 reported that vertically-suspended structures (aluminium angles) in tanks, combined with an exercise routine, may be beneficial during the rearing of juvenile landlocked fall Chinook salmon. On the other hand, an experiment on brown trout, chinook salmon and Atlantic salmon reared in circular tanks with vertically-suspended aluminium rods as enrichment structures did not show any effect on growth for any species, probably due to the short experimental period or underfed fish.57 Moreover, colours of vertically-suspended structures seemed to have no relevant effects on growth performance of hatchery-reared chinook salmon and rainbow trout.67,68 This highlights the need to
provide ethologically relevant EE features to the species of interest, under the risk of null or even negative effects. Vertically suspended plant-fibre ropes can also be successfully used as an EE strategy for farmed fish, as it has been demonstrated for gilthead seabream.69-71 Arechava- Lopez et al.69 demonstrated that such simple structures can reduce aggressiveness in juvenile seabream and modify the distribution of fish, leading to better fin condition and less interactions with the net pen (e.g. less bites and fins rubbing), but no effects were reported on fish condition, growth and mortality. Arechava-Lopez et al.70 showed that vertical ropes can enhance seabream cognition, exploratory behaviour and brain physiological functions. Suspended ropes were also applied in experimental sea-cages of on-growing seabream, which increased their spatial use in the net-pen, so such ropes were recommended as a passive and non-invasive tool for improving welfare of intensively cultured seabream.71

2.1.2 | Substrates

Providing floor substrate (sand, pebbles, gravel, stones, etc.) can be seen as another type of physical EE to improve or guarantee the welfare of fish,23,24 mostly for those species that regularly interact with the bottom or live closely associated to it during its whole life (e.g. benthic fish). For example, flatfish are benthic organisms inhabiting sandy or muddy bottoms, but are commonly cultured in smooth-substrate tanks where they often develop skin lesions on the blind (abocular) side, decreasing their welfare, but also causing economic losses to the farmers.72-75 Therefore, adding substrate to the tanks could address some of the biological needs of these species and/or provide some welfare benefits. Dou et al.76 reported an increase in resting behaviour, a reduction of metabolic rate and a decrease in cannibalism in olive flounder (Paralichthys olivaceus) after adding gravel to the bottom of the rearing tank wherein fish can bury themselves or hide. Studies on the Atlantic halibut (Hippoglossus hippoglossus) showed that substrate-covered bottoms (e.g. sand, gravel) can reduce skin lesions, infections and hyperpigmentation.73,77 Ambicolouration or blind-side hypermelanosis on olive flounder and starry flounder (Platichthys stellatus) can be also reduced, or even eliminated, by providing gravel as substrate enrichment in rearing tanks.74,79,80 Furthermore, sandy substrates in tanks also play an important role as a prophylactic measure and even for the treatment of skin diseases, for example in Dover sole (Solea solea),72,81 whereas improving plain cement bottoms by blending with silica fume (10%) improves growth, fin erosion, skin lesions and abnormal pigmentation patterns in Senegalese sole (Solea senegalensis).82 Reiser et al.83 found that natural and artificial substrate enrichment can modulate epigenetic patterns in rainbow trout, affecting global DNA methylation in the brain at the egg and alevin stage, the period during development where the animals are in close physical contact with the substrate. Additionally, cobble substrates provided in concrete raceways can improve fin condition and decrease related infections of rainbow trout and cutthroat trout (Oncorhynchus clarkii).84-86 Similarly, artificial seaweed (AquaMats®), specifically designed to provide structural enrichment in pond bottoms, improve the growth and fin condition of rainbow trout, whilst allowing the growth of aquatic plants and invertebrates as an additional nutritional source to cultured species.87

The gilthead seabream is a demersal species that usually forages on the bottom substrate. Some studies on juveniles revealed that adding a uniform layer of single colour glass gravel as enrichment in rearing tanks can induce positive effects on fish condition and growth performance (i.e. final mass, specific growth rate, mass gain, food conversion ratio), and also reduces aggressiveness, increases fish-bottom interactions, improves the stress response (reduce brain serotonergic activity) and promotes better fillet quality.88-91 Therefore, although different bottom colours and densities can lead to different effects (see Sections 2.2 and 2.4 respectively), these authors pointed out that improvement of the fish rearing environment with substrate may have multiple beneficial aspects for both fish welfare and producers. Murtaza et al.92 reported a significant benefit of enriched early rearing environment (including multi-coloured gravel substrate, cobbles and plants) on the physiologic stress response to net capture and confinement of grass carp (Ctenopharyngodon idella). Authors recommended the use of this kind of EE to produce fish with better ability to cope with stressful events.92 Similarly, Tatemoto et al.73 demonstrated through novel-object tests that substrate in more complex environments (i.e. mostly gravel substrate with some glass balls and small coloured PVC pipes) improves the affective states and welfare of Nile tilapia.

Substrate enrichment can also be applied to incubation processes. Salmonid alevins (yolk-sac fry) hatch from eggs buried in gravel and spend the first stage of their life within this substrate. Adding hatching mats to the bottom of the tanks provides a wide range of positive effects, as it has been demonstrated on different salmonid species (e.g.23,98). These hatching mats improve growth and survival of alevins, reduce yolk-sac constrictions and improve yolk conversion efficiency, reduce alevins swimming activity and malformations and permit resting on the bottom in normal body-position. Hatching mats also promote positive physiological changes, increase brain growth and decrease high activity and oxygen consumption due to stress.23 Indeed, several commercial salmon hatching mats are already available.16

Similar positive effects on hatchlings have been shown for Atlantic sturgeon (Acipenser oxyrinchus) and white sturgeon (A. transmontanus) when adding sand and gravel to the bottom of the tanks as incubation substrate.93-97 Substrate plays a crucial role in many cichlid species that exhibit substrate-oriented activities during the breeding season, such as males digging pits or nests in soft bottoms, displaying courtship behaviours to attract females and establishing territories.98 Male Nile tilapia prefer small-grained gravel or sand substrate to stones to dig spawning nests.99,100 In the case of Mozambique tilapia (Oreochromis mossambicus), sandy bottoms can reduce aggressiveness during courtship and nest-building and, therefore, reduce stress and increase welfare of breeding males.101,102 Altogether, these studies reveal that the lack of
substrate is particularly deleterious in a reproductive context for these species and, thus, it is likely to decrease the welfare state of breeding fish and hatchling offspring.

### 2.1.3 Combinations

Physical EE can provide shelter, substrate and complexity in a rearing environment at the same time, and can also allow the co-habitation of different species. This is the case of enrichment structures for cleaner-fish in salmon aquaculture. Lumpfish (Cyclopterus lumpus) and several wrasse species (e.g., *Labrus bergylta*, *Ctenolabrus rupestris*, *Centrolabrus exoletus*, *Symphodus melops*, *Labrus mixtus*, *Tautogolabrus adspersus*) are the most common cleaner-fish currently used as a biological control for sea lice on farmed salmon (sea-cages) in Europe and Canada.\(^\text{102}\) The use of cleaner-fish seems to be an alternative method of louse control, but for it to be efficient and ethical, the health and welfare of the cleaner-fish is also of major importance.\(^\text{104}\)

Juvenile lumpfish are typically found amongst kelp during their first year of life, both attached and free floating; therefore, those stocked in commercial salmon cages will need some type of shelter or substrate to attach to when resting, and to shelter to during periods of inactivity or adverse environmental conditions.\(^\text{102}\) Imsland et al.\(^\text{105}\) demonstrated that juvenile lumpfish are able to adhere and rest on smooth flat vertical or floating plastic surfaces, which may mimic their natural requirements for surface adhesion. Structures made of pipes or artificial kelp are also provided to wrasse stocked in commercial salmon cages, providing shelter and resting hides for their overnight inactivity.\(^\text{103,106}\) Consequently, and given the quick expansion of the use of cleaner-fish in commercial salmon cages, several companies manufacture a varied range of vertical substrates or ‘kelp curtains’, resembling artificial kelp made of PVC.\(^\text{103}\) In this line, Leclercq et al.\(^\text{106}\) developed sinking hides of plastic fake-kelp for ballan wrasse (*L. bergylta*) stocked in commercial salmon cages. These structures had hanging feeders or ‘feed blocks’ (water-stable agar-based diet on PVC pipes or trays), forming altogether a complex vertically suspended shelter and supplementary feeding for cleaner fish. These feed blocks were also specially designed for lumpfish—which quickly accepted and grazed on them—and supplementary pelleted-commercial feed.\(^\text{107,108}\) Kelp-curtains, shelters and feed-blocks can be used for any cleaner-fishes in farming conditions. However, it is important to highlight that, given the behavioural and biological differences amongst species,\(^\text{109,110}\) they must be specifically designed for each cleaner-fish species. Moreover, the farming strategies and rearing conditions should also be taken into account to avoid undesirable effects.\(^\text{111}\) A further point worth considering when providing kelp-curtains, shelters, and feed-blocks for cleaner-fish that coexist with Atlantic salmon in commercial cages, is that the complexity of the rearing environment is increased for both species and, of course, such provided structures must not cause any detrimental effect to either co-habitant’s welfare.

Another example of physical EE combining both structures and substrates is periphyton-based aquaculture.\(^\text{23}\) Periphyton is a matrix of bacteria, algae and microorganisms embedded in a mucopolysaccharide matrix that colonises structures placed in earthen ponds, and that can be consumed by fish, increasing the productivity and efficiency of aquaculture systems.\(^\text{112}\) Application of periphyton structures can be mostly found in Asian and African ponds rearing cichlids or cyprinids. Periphyton structures can be made of organic materials, such as bamboo, rice straw or sugarcane fibrous matter or made with PVC pipes or plastic slides, but the former provide higher benefits in of growth, immunity and survival.\(^\text{112}\) To summarise, physical EE is probably the main type of EE to be considered in fish farming, but the fundamental questions surrounding their deployment (what type, how much, when and how) should be answered in advanced.\(^\text{24}\) It is therefore important to consider the nuances and details of its implementation, which should first and foremost consider the ethology of the species in question,\(^\text{5}\) and consequently the functional relevance on the physical structures to be implemented.

### 2.2 Sensorial enrichment

In the wild, animals are exposed to an ever-changing array of sensory stimuli that triggers the diverse senses of fish, whereas captive environments are generally much more deficient in terms of the sensory cues.\(^\text{113}\) However, to successfully provide sensory stimuli and implement sensorial EE in captive environments, it is essential to have a good knowledge of the biological needs and the sensory worlds of the targeted species.\(^\text{5}\) This is especially relevant for fish, given that there are substantial differences in their sensory systems compared to terrestrial animals, due to differing ecological and evolutionary pressures.\(^\text{15}\) In order to promote better welfare of captive fish, different sensory stimulation must be explored as potential methods of EE for these animals, including visual, auditory, chemical (olfactory, taste), hydromechanical and electrical stimuli.

#### 2.2.1 Visual stimuli: lighting, covers and colours

Light is a key environmental factor that synchronises all life-stages of fish, from embryonic development to sexual maturation.\(^\text{114}\) Some researchers have extensively explored the effects of light characteristics (periodicity, intensity, spectrum) in a wide variety of species, life-stages and rearing environments, suggesting different strategies of sensorial enrichment through visual stimuli. The diversity of fish visual systems, which might change during their life-history, or even within life stages, together with the enormous variety in eye anatomy and brain structures that process visual information,\(^\text{115,116}\) make visual enrichment very challenging. In addition, light behaves differently underwater than at the surface, and can not only be influenced by many physical and biological factors, but also fluctuates within daytime, season or natural weather conditions.\(^\text{5}\) At indoor fish-farm facilities, however, farmers can simulate natural light conditions to
promote natural chronobiology, although artificial lights may differ greatly from natural solar light.\textsuperscript{117} Classic light bulbs (incandescent filaments) produce a reddish inefficient light underwater, whilst fluorescent tubes produce sharp peaks at specific wavelengths far from natural daylight, but modern light-emitting diode (LED) technology provides versatile and better cost-effective lighting systems which can be used for different purposes in aquatic research and captive environments.\textsuperscript{118} Overall, efficiency of production and quality of aquacultural products can be improved if the activities of fish husbandry are timed to coincide with the biological rhythms of fish.\textsuperscript{119}

Light characteristics (intensity and spectrum) and circadian clock (periodicity) represent key regulators of many aspects of fish biology. They can be artificially controlled and are frequently manipulated as part of strategies designed to maximise productivity in fish farms, but can also be used to guarantee good welfare conditions. In fact, the species-specific behavioural and physiological responses to acute stressors depend heavily on the time of the day when the stress occurs; this has been extensively reported in many species of farming interest.\textsuperscript{117} The effects of environmental cycles, biological rhythms and artificial lighting conditions during early development have been extensively studied and reviewed for many species of commercial interest.\textsuperscript{117,120,121} In general, the overall performance, development and welfare of fish larvae are significantly affected by light characteristics, obtaining better results under the closest conditions to their natural environment.\textsuperscript{117} Juvenile and adult fish also present daily cycles of locomotor and food anticipatory activities, which are directly affected by lighting conditions.\textsuperscript{122} Therefore, understanding the circadian timing system of fish is essential for optimization of rearing protocols and the improvement of their well-being in farming environments.

Similarly, light spectrum might have physiological and behavioural effects on fish in captivity. In the underwater environment, the spectral composition of both solar and artificial radiation changes greatly and is absorbed differently by the water column.\textsuperscript{123} Therefore, shortwave radiation (violet and blue) diffuses more, whilst longwave radiation (red and orange) diffuses less.\textsuperscript{123} For early developmental stages, juveniles and breeders, it is generally recommended providing short wavelength lights (blue and/or green colours) which, in combination with proper light periodicity and intensity, induces positive effects on growth and performance, enhances locomotor and feeding activity, reduces stress and mortalities, promotes spawning behaviour and affects organoleptic properties.\textsuperscript{117,120,124} Moreover, the antibacterial and anti-protozoal activities of blue LED light-emitting diode light (405-465 nm) have been demonstrated for some farmed species, without apparently causing side effects (in contrast to UV light).\textsuperscript{125,126} Therefore, it is recommended avoiding long wavelength light (red colour), as well as constant light or constant darkness, which negatively affects fish welfare in terms of embryo, larvae and juvenile development, spawning, malformations, eye damages and mortality.\textsuperscript{117}

Some studies on the Atlantic salmon have also reported direct effects on behaviour induced by light intensity and positioning in cages.\textsuperscript{127-129} Herbert et al.\textsuperscript{127} applied a central lighting device that provided an apparently moving light pattern to induce sustained exercise in salmon, which enhanced growth rates and feed conversion, and reduced plasma cortisol. On the other hand, Bui et al.\textsuperscript{128} reported that fish groups exposed to high and medium intensity of blue LED light showed a marked change in vertical distribution, displaying erratic swimming and increasing surface activity, both symptoms of stress. Wright et al.\textsuperscript{129} showed how Atlantic salmon instantaneously follow vertical light movements in sea cages. The authors suggested that positioning of lights may help move salmon away from fluctuating unsuitable depths (e.g. lice-rich depths) into temporary favourable depths (e.g. surface brackish waters to treat against stenohaline parasites), and throughout cages to avoid crowding in narrow depth ranges. However, responses to different light conditions may vary depending on the species, especially due to specific physiological needs or behaviours (e.g. phototaxis), and also on the adaptation to different environments within the same species (e.g. living at different latitudes).

Likewise, covers can be used to modify lighting conditions in a more indirect way, reducing the amount of light and providing shades. Several studies on salmonids demonstrated that the use of covers can prevent sun-burn and UVR-induced effects, whilst also preventing jump-out and predation, improving fish performance and reducing stress (e.g.\textsuperscript{130-138}). Most of these studies pointed towards partially covered environments as the most beneficial for fish performance and welfare. A recent study on Nile tilapia, however, showed that providing partially covered conditions in rearing tanks can induce stressful conditions, compared to fully covered or uncovered tanks.\textsuperscript{139} Rearing tanks can be manufactured in a wide variety of colours, offering high flexibility to aquaculture production, considering that most cultured fish can distinguish colour and thus be affected by the colour of their rearing environment. Tank colour and depth, together with light source and water clarity, impact the degree at which light is absorbed, reflected, scattered and attenuated in the rearing environment. McLean\textsuperscript{25} reviewed the effects that tank colour (floor and walls) may have on various physiological and behavioural processes in larval and post-larval fishes. The author compiled a vast number of studies on a wide range of species demonstrating that different background colours can influence fish performance and survival, health, level of stress and even level of aggressiveness; effects that can be negative or positive depending on species and life-stage.\textsuperscript{25} Diverse patterns of wall and bottom tanks can be also applied as sensory enrichment, stimulating the visual system. For example, studies on Pacific bluefin tuna (Thunnus orientalis) reported that coloured wall patterns (lattice and polka dot coloured patterns) increased the survival of juveniles during growing and transportation, decreasing collisions, bone injuries and physiological stress.\textsuperscript{140,141} Similarly, striped coloured walls and lattice coloured bottoms were successfully applied on rearing tanks of juvenile Atlantic bluefin tuna (Thunnus thynnus) to modify swimming activity, reducing collisions and, consequently, injuries and mortalities.\textsuperscript{142} Additionally, fish pigmentation is also strongly influenced by background colour, which can lead to significant consequences at consumer levels, mostly for species sold skin-on whole/gutted.\textsuperscript{25}
Some research has indicated the potential use of mirrors and other reflective devices as a method for visual stimulation or enrichment for captive animals, particularly for individuals subject to social isolation. However, in the case of aquaculture, fish are not reared in isolation and the use of mirrors is not recommended, since they may induce negative effects. For example, mirror images simulate intrusions in territorial fish (e.g. cichlids), triggering aggressive responses with their mirror image in unresolved disputes, which can lead to dysfunctional or even fearful states. A recent study, using a complex operant conditioning device, demonstrated that rainbow trout are able to discriminate 2-D photographs of conspecifics from different visual stimuli, suggesting the positive effects of developing visual-based enrichments for fish cognition. Therefore, there is ample scientific evidence that the use of visual stimuli as sensory enrichment can induce positive effects on fish welfare, despite the existence of important differences amongst light and colour sources, and species. However, the potential adverse effects of light systems, protocols and background colours need to be assessed before implementing their use in aquaculture settings, ensuring that animal welfare is not compromised.

### 2.2.2 Auditory stimuli: noise and music

Human activities in aquatic environments generate a wide range of waterborne noises and, consequently, fish are subjected to extreme levels of acute (transient) and chronic (continuous) noise, both in natural and cultured conditions, which may negatively affect their stress level and welfare. Auditory capabilities and processing mechanisms of fish are highly sensitive and complex and differ amongst species. In natural waters, human activities are the source of a wide range of sounds, generating acoustic stresses that are particularly important in coastal zones, where most of the sea-based aquaculture facilities are located. For example, underwater anthropogenic-derived noise (i.e. urban and shipping noise, drilling and piling) negatively affects the behaviour (swimming activity, group cohesion, distribution) and physiology (primary and secondary stress responses) of gilthead seabream and European seabass. Negative behavioural effects of anthropogenic-derived noise (i.e. infrasound, surface disturbances, urban and shipping noises) were also reported on Atlantic salmon and Nile tilapia. In addition, an even greater amount of noise is generated in land-based aquaculture systems, especially in enclosed recirculation systems.

High-frequency noise (1–2 kHz) is mostly generated by electrical motors, oscillating and collapsing air bubbles, aeration and water pump action, whereas low-frequency noise (25–1000 Hz), which is within the hearing range of most teleosts, is generated by water flows, ground vibrations, tank wall vibrations and electrical pumps. Therefore, it is essential to take the appropriate measures (e.g. isolation and proper materials, spatial planning, etc.) to reduce background noise-related impacts, ensuring good welfare conditions of farmed fish. This approach might be considered a strategy closely related to a kind of sensory enrichment, since it masks or reduces negative auditory stimuli. This reduction of background noise might also allow better communication through naturally-generated sounds of the captive species, which are produced in various behavioural contexts (agonistic interactions, courtship, spawning, distress). On the other hand, adding background sounds specific to a species’ natural habitat is already considered an EE strategy through sensory stimulation in captive animals, and even though some studies suggested the potential use of sea soundscape, further studies are needed in this matter.

In addition, recognition of the direct effects associated with music for human well-being has prompted recent research into the value of auditory stimulation as a means of enriching the environment of captive animals, ultimately with the view of meeting one or more of the suggested goals of EE. In this sense, some studies have assessed the potential effects of adding background music (i.e. rhythmic or systematic sound not typically found in the wild) on cultured fish. For example, it has been demonstrated that musical stimuli positively influence growth performance, feeding efficiency and stress reduction on common carp, gilthead seabream and rainbow trout, mostly reared in recirculating water systems. Similarly, Catli et al. reported that slow tempo music-induced positive effects on growth performance and feed intake of turbot, whereas fast tempo music-induced negative effects and stress in this species. Therefore, musical stimuli can be regarded as a stress relieving or inducing factor, but adequate selection of tempo, frequency and harmony may enhance welfare and can be applied as a sensorial enrichment strategy in intensive aquaculture facilities. Overall, further studies are still needed, systematically exploring both behavioural and physiological effects of different auditory stimuli on a wider range of species at different developmental stages and environments.

### 2.2.3 Chemical stimuli: olfaction, taste and chemosensing

Chemical senses play an essential ecological role (fish-environment interactions) and are extremely relevant in communication contexts in all fish taxa (cyclostomes, elasmobranchs and teleosts). Chemical sensing in fish is highly particular compared to terrestrial animals and exists in three modalities, the importance of which depends on species and life-stage: olfaction, taste and solitary chemosensory cells. Chemical sensing is fundamental for intra-specific communication in fish, allowing not only males and females to find suitable partners, but also the assessment and announcement of status in agonistic contexts, which are solved much quicker and less violently thanks to ‘chemical diplomacy’. On the other hand, chemical sensing also enables fish orientation and inter-specific interactions, such as predation, territorial aggressions, foraging and escaping from predators in dark or murky waters. Biological waterborne chemical signals are ubiquitous in aquaculture systems, being released in agonistic encounters, during handling, feeding or breeding, and are prevalent at high stocking densities. A build-up of chemical
Tactile stimuli and other sensory systems

Fish are widely covered by tactile receptors and may also possess various tactile organs, mostly cutaneous outgrowths (e.g., barbels, free rays of fins, rostrum, breeding tubercles, or dermal teeth). Tactile organs are highly significant in orientation, reproduction, defence, social interactions, exploration and food searching behaviour. The fins have been found to function as proprioceptors, by providing feedback on fin ray position and movement, and as tactile sensors, by encoding pressures applied to the fin surface. Intra-oral tactile reception also has an important role in estimating the texture and attractiveness of food objects. It is also known that cleaner-fish provide tactile stimulation with the pelvic and pectoral fins to their clients in coral reefs. This tactile stimulation is beneficial for clients, by lowering their stress and removing parasites, and dead and infected tissues, and for cleaners, by helping to keep clients available for longer and reducing conflicts. In aquaculture, however, whether the tactile stimulation of cleaner-fish (e.g., lumpfish and some wrasse species) reduces the stress and social conflicts on the clients (i.e. salmonids) or not, remains to be proven. Recent studies on Nile tilapia suggest that, although tactile stimulation does not lower blood cortisol levels in the short-term, it can reduce aggressiveness and may also reduce the overall stress associated with social interactions in long-term. Moreover, a recent study reported that koi carp (Cyprinus rubrofuscus) showed interest in physical contact (tactile interaction) with humans, suggesting that interacting with human skin, a novel substance and texture, might serve as a source of tactile and/or sensory enrichment. However, further studies are still needed to test several effects of tactile stimulation on fish welfare.

There are other sensory systems, such as hydromechanical and electro-sensing, which are involved in diverse biological and ecological functions. Fish are able to detect and perceive the hydrodynamic and physical environment they inhabit and process this sensory information through their mechanosensory lateral-line system. The lateral-line system consists of up to several thousand neuromasts distributed across the entire body of the animal. Using the lateral-line system, fishes perceive water movements (i.e., hydrodynamic stimuli) of both biotic and abiotic origin, such as those generated by conspecifics, predators and prey, and therefore acting as a communication tool. In addition, electro-sensing is present in certain teleost species, being able to detect electric fields from a multitude of sources, including the earth’s magnetic field and the bodies of all aquatic organisms including the electro-sensing fish itself. The extremely high sensitivity of fish to these fields enables orientation, navigation, communication and even detection and localization of other fish, both prey and conspecifics. Nevertheless, the stimulation of these last sensory systems in captivity is not yet assessed, and may be indirectly addressed through other enrichment strategies, such as social, occupational, or even physical enrichment, as well as by good welfare practices and management at fish farms.
2.3 | Occupational enrichment

In nature, fish are continuously exposed to physical and psychological challenges and, therefore, occupational EE aims to introduce diverse challenges into the rearing environment that are important to prevent monotony and, consequently, boredom. Occupational enrichment can encompass psychological devices that provide animals with challenges or control over their environment, as well as enrichment encouraging physical exercise.210

2.3.1 | Hydrodynamism: flow, currents, and exercise

The exercise levels and swimming capacity of fish cultured in ponds, recirculating systems, raceways and cages are generally lower than those in the wild, but depend heavily on species, life-stage of development, and rearing systems. The study of fluid dynamics (water flows, currents, waves, etc.) within aquaculture facilities, and how it influences swimming behaviour, has proven to be of great importance for designing captive environments, both on-land and offshore cage systems.211,212 Some studies on Atlantic salmon open-sea cages, where the fish can be exposed to diverse environmental challenges, demonstrated that waves and currents have a direct effect on the group shoaling behaviour and distribution inside the net-pen.213,214 Similarly, turbulence and water flow in land-based systems have been shown to have both positive and negative effects on fish swimming, feeding and energetics, usually with negative impacts at very low and at high levels, with least effects and, sometimes, positive ones at intermediate levels.215

Forcing the fish to swim in a certain water-flow can promote swimming exercise and could represent a natural, non-invasive, and economical approach to improve growth, resilience, robustness and welfare.216 Optimal exercise may have beneficial effects of major importance for aquaculture and, therefore, is a potential occupational enrichment strategy to be considered by the industry. Exercise-induced growth is optimal at specific speeds, most likely near optimal swimming speeds ($U_{opt}$) where the cost of transport is the lowest and the energetic efficiency is the highest.216 At swimming speeds lower than $U_{opt}$, energy is lost due to higher spontaneous activities (e.g. flight responses), whilst at higher speeds, swimming becomes unsustainable, stressful, and can finally cause fatigue.217 It must be noted that critical swimming speed varies with group shoaling behaviour,218 and also that fish densities and other structures can alter the water flow.219,220

In salmonid fish, the stimulatory effects of sustained moderate swimming on growth performance have been widely demonstrated. When juvenile salmonids are reared in flowing water (0.75–1.5 body length per second; BL s$^{-1}$), they tend to grow faster, making more efficient use of the food and showing uniformity of growth rates and a reduced size range at harvest.221 Some studies on Artic char (Salvelinus alpinus) also showed that exercised fish presented not only better growth performance, but also different body composition (lower fat and higher protein) than control fish.222,223 An increase in swimming speed caused a marked increase in schooling behaviour and lower levels of aggressive interactions, but the moderately exercised fish presented the highest growth performance. Additionally, Herbert et al.227 induced sustained exercise in Atlantic salmon using a lighting device centrally placed in semi-commercial tanks that provided an apparently moving light pattern. Exercised salmon (exposed to 1.5 BL s$^{-1}$) presented enhanced rates of growth and feed conversion, and reduced levels of plasma cortisol, improving productivity and welfare. Water current velocities can be also regulated in closed containment systems (e.g. closing cages) placed in the sea. Nilsen et al.224 demonstrated that moderate water velocity (0.36–0.63 BL s$^{-1}$) can be favourable for growth rates and performance of post-smolt Atlantic salmon during the entire on-growing period in commercial closed contained systems.

Contradictory effects of water flow are also reported. More recent studies on chinook salmon and rainbow trout reported lack of positive effects on growth performance and post-transportation stress response between fish reared at different water flows.225,226 The authors indicated that a moderate velocity (1.5 BL s$^{-1}$), which is necessary for circular tanks to be self-cleaning, is not detrimental to fish growth or condition, whereas a faster water velocity (3.0 BL s$^{-1}$) may negatively affect fish growth and food utilization in the long-term.227 They also highlighted the importance of pairing exercise with adequate food intake to avoid undesired effects.228 Similarly, no clear effects on growth performance were reported on exercised rainbow trout under intermittent or constant water-flow regimens, combined with vertically-suspended structural enrichment, which directly influences the water flow.58,61,64,66 However, a combination of structural enrichment and water-flow is important for fish habitat preference and, therefore, the potential effects of multiple factors simultaneously deserve further attention.227 Villarol et al.228 found no evidence of positive effects of water-induced exercise on growth performance and growth of rainbow trout. However, exercised fish presented a better adaptation to acute stress. Reiser et al.229 reared juvenile brown and rainbow trout in commercial earthen ponds exposing fish to a sustained swimming condition, by using paddle-wheel aerators to create circular flow patterns with a range of current speeds in the system at minimal or no additional costs. Brown trout reared with that current had higher protein and lower fat, but no effects were observed on growth, whereas water current positively affected the growth of rainbow trout that presented lower fat and lower energy.229

Much less information is available on the potential stimulatory effects of swimming exercise in non-salmonid species. Ibarz et al.230 showed that swimming exercise stimulates growth in gillhead seabream. Palstra et al.231 demonstrated that, in the same species, water flow-induced swimming exercise near $U_{opt}$ (at 1 BL s$^{-1}$) provided optimal conditions for growth and uniformity, but also physiological stress, robustness and energy mobilisation. However, the percentage of lordotic fish increased with exercise and the authors suggested that exposing fish to random waters currents (instead of constant flows) could bring welfare benefits.232 Shi et al.232 demonstrated that sustained swimming training have direct effects on filet...
texture of European seabass. Moreover, different flow velocities had significant effects on the growth, digestive enzyme activities, antioxidant capabilities, and immune capabilities of juvenile large-mouth bass (*Micropterus salmoides*) in recirculating systems (RAS).\(^{233}\) A study on Nile tilapia showed that water flow can help the fish to cope better with stressful events, such as being introduced into novel environments.\(^{234}\) In addition, optimal exercise may also have beneficial effects on reproduction control.\(^{216}\) Swimming exercise may thus represent a way to significantly control puberty in farmed fish,\(^{235}\) at least amongst female migrant anguilids (e.g. *Anguilla anguilla*) besides salmonids. Induced-swimming exercise can trigger lipid mobilisation, delay of sexual maturation, prevent precocious maturation, and extend the growth period.\(^{216}\) Therefore, together with induced growth, enhanced flesh quality, increased survival, robustness and fitness and increase welfare by lowered stress, the potential benefits of this type of occupational enrichment deserves further attention by the industry.

### 2.3.2 Predictability and variability

Fish are exposed to highly variable environmental stimuli and challenges in the wild. Some are unpredictable, such as predation risks, food availability and human threats. Other external stimuli can be somehow predictable, presenting temporal patterns and constant fluctuations, such as solar and lunar cycles, tides, and daily temperature variations. The right amount of environmental predictability reduces the uncertainty that animals are exposed to, improves their cognitive skills, such as learning and spatial memory, and favours engrained behaviours.\(^{236}\) However, human-induced environmental predictability can create evolutionary traps that are detrimental to an animal’s fitness; for example, predictable feeding induces high competition and thereby increases dangerous or lethal injuries.\(^{237}\) Thus, when having fish in captivity, the right balance between predictability and uncertainty is necessary, adjusting the variability within predictable events to ensure that animals do not get accustomed to the same exact routines, and thus do not reach allostatic overload when they are exposed to unpredictable events.\(^{238}\)

Fish learn to predict events when they always take place at the same time of the day.\(^{239-241}\) Several studies have shown that fish can be trained to predict events via classical conditioning.\(^{242-246}\) Thus, fish can be trained to predict negative events and then habituate to stressors, inducing a low physiological stress response, as shown in Atlantic salmon parr.\(^{247}\) On the other hand, predictability of a positive event, such as feeding, can be detrimental for the welfare of fish in some species, such as Atlantic salmon parr, to which it induces higher levels of aggression.\(^{240}\) Moreover, spatially and temporally predictable feeding regimes in brown trout induced aggression and territoriality, which increased growth in individuals with high resting metabolic rate.\(^{243}\) However, implementing unpredictable feeding regimes as an alternative strategy can also be detrimental to welfare. For example, in Atlantic salmon parr, this generated a dissociation of roles within their network, with heavier and longer fish initiating attacks towards smaller individuals, which had higher dorsal fin damage as a consequence.\(^{240}\) In gilthead seabream, an unpredictable feeding regime was also detrimental for welfare, since it increased cortisol and glucose, and overall locomotor activity which, together, suggests that unpredictability induces stress.\(^{239}\)

All these studies bring forward the importance of considering the stimulus valence (i.e. whether a stimulus is positive or negative) when studying stimulus salience (i.e. whether it is predictable or unpredictable). In fact, several studies have shown that the different combinations of valence and salience of a stimulus have different effects in the behaviour of fish,\(^{242}\) as well as in their physiological and neuromolecular states.\(^{243,244}\) For example, in gilthead seabream, appetitive stimuli (feeding) promoted social interactions, aversive stimuli (physical constraint) triggered escape attempts, and predictability increased the frequency of these behaviours in contrast to unpredictability. The same authors found that aversive stimuli increased cortisol levels compared to appetitive stimuli, and unpredictability elicited higher cortisol levels compared to predictable regimes. More importantly, each experimental treatment (appetitive-predictable, appetitive-unpredictable, aversive-predictable, and aversive-unpredictable) generated different patterns of gene expression in three brain regions related to reward and aversion processing.\(^{242}\) This study shows that both the valence and the salience of the stimulus affect the behaviour, physiology and neural activation of fish in different ways, inducing emotion-like states. Cerqueira et al.\(^{244}\) showed in European seabass that an unpredictable negative stimulus (confinement) increased shoal cohesion and freezing and escape behaviours, reduced exploratory behaviour and increased cortisol levels and neural activation of the dorsomedial telencephalon (putative telost homologue of the mammalian amygdala) compared to a predictable negative stimulus, meaning that an unpredictable stressor triggers a stress response in this species. Similarly, Galhardo et al.\(^{242}\) showed that Mozambique tilapia trained to predict a negative event (confinement) showed lower stress-related signs than a group exposed to an unpredictable visual sign and had lower cortisol levels during isolation. Alternatively, when exposed to a positive event (feeding) the fish trained to predict it showed higher anticipatory behaviour and activity compared to the fish exposed to the unpredictable sign, and the latter had lower cortisol levels compared to their baseline levels.\(^{242}\) The authors discussed that anticipatory behaviour might be linked to negative emotions, generating expectations, frustrations and loss of control. In fact, in a study on Atlantic salmon, omission for 30 minutes of an expected reward induced higher levels of aggression and a stronger hierarchical conformation of the group, although this change in behaviour did not result in changes of cortisol levels.\(^{245}\) Furthermore, the omission of an expected reward can affect not only the behaviour, but also the biochemistry and structural organisation of the brain.\(^{246}\) Overall, these studies show that both predictable and unpredictable conditions in the environments have the potential to create welfare issues, and thus a balance between the two (i.e. adding certain variability to a predictable environment) may be a solution, although further research is needed to confirm this hypothesis.
In this line, a good way of preparing adult fish to the unpredictability of their environments, both in farms and natural habitats, is adding environmental variability to their rearing setup during their growing stages. For example, hatchery-reared Atlantic cod raised in barren environments receive more attacks, flee more often and have a lower shelter-use than conspecifics reared in variable enriched environments. Similarly, early exposure to variable spatial cues and food regimes generated Atlantic cod more attracted to live prey and faster consumption, with lower latency to explore novel areas, and with faster recovery from a stressful event compared to those reared in barren environments. An unpredictable food regime also alters the development of European sea bass, which grew slower and were bolder than conspecifics raised in a predictable feeding schedule. In Atlantic salmon parr, adding shelter and variability in the water level and direction and velocity of the currents at production-scale densities increased the feeding rates on natural prey, and in smolts, these rearing conditions increased migration speed and survival rate in the wild. Therefore, fish raised in environments with some degree of variability seem to learn and develop flexible behaviour that better prepares them to confront environmental unpredictability compared with fish raised in barren environments. However, spatial variability of the enrichment might not be beneficial for all species. For example, a study on steelhead trout (O. mykiss) showed that those exposed to 4 weeks of stable EE had lower latency to explore a novel environment compared to steelhead trouts exposed to either unstable EE or to barren environments. The data dispersion of the steelhead trouts raised in unstable-enriched and barren environments were higher compared to the ones raised in stable EE, which might indicate that the former environmental situations might promote a wider behavioural repertoire, which could include unnatural or maladaptive behaviours. Although the differences between the steelhead trout studies and the previously mentioned research may be due to differences in methodology, it is nonetheless important to test the effects of EE variability in the species of interest before implementing a programme to ensure that the added variability will promote a suitable behavioural repertoire and positive welfare.

2.3.3 Play and joy

Play is defined as the voluntary and repetitive manipulation of a non-food object, excluding instances of intention/purpose. In this sense, some fish species display behaviours likely to involve positively valenced experiences, or even likely to have the ability to play. Various studies identified three different play behaviour subtypes in fishes: locomotor (e.g. bubble jets/air stone), object manipulation (novel/stimulatory) and social (including human interaction). Regarding species of aquaculture interest, it is known that salmonids and other fishes can jump into the air from the water, which is highly relevant in net-pen culture since this behaviour can be related to buoyancy regulation, parasitic infections or stress. However, Fagen suggested that some salmonid jumping behaviour may be also a form of play. Encouraging play behaviour, therefore, might be considered as occupational EE, though whether it involves positive emotions in fish is still under debate, and further research is still needed in this field.

2.4 Social enrichment

Social enrichment comprises not only the presence of other individuals and their social interactions, but also the availability of space to interact or avoid other fish, either conspecifics or different species. In this sense, it is important to know whether the reared species is solitary, or likely to shoal in small or big groups at different life-stages, as well as if they usually co-habit with other fish species in the wild. For example, many fish species form shoals in the wild and, thus, in captivity, these species may suffer in isolation or in inappropriate spaces to properly shoal. On the other hand, most farmed species that do not shoal in the wild, or associate with other species, are territorial and can engage in aggressive behaviours with conspecifics, which in both cases may be a big problem in the high stocking densities of captive environments.

Stocking density is one of the major aspects to consider in improving fish welfare in monospecific intensive aquaculture, which is the most widespread practice. Diverse studies have demonstrated that different stocking densities can have direct effects on the stress response, growth rate, health and condition of intensively farmed fish. For example, in most farmed fish species, lower densities can improve growth rates and fin condition, reduce injuries, promote a better stress response and increase size-homogeneity, and may also lead to positive effects on fish distribution and spatial use. Nevertheless, discrepancies found within the literature have highlighted that the effects of stocking density are complex and appear to consist of numerous interacting and case-specific factors and, therefore, require careful consideration. For example, Adams et al. reported that both low and high densities can compromise welfare in Atlantic salmon, and the overall welfare was best at an intermediate density. Appropriate density depends heavily on the behavioural and physiological requirements of each farmed species, as well as on life-stage, rearing system, food availability, social interactions and other environmental parameters (i.e. variations and alterations of water quality). Some species, such as catfish species, can tolerate high stocking densities in different farming systems. Farming catfish at high densities can lead to higher net fish yields and financial benefits, but exceeding specific stocking densities can also lead to impaired welfare (e.g. skin lessons, infections, mortalities) and problems to ensure long-term sustainability. Even low stocking densities can have negative effects on welfare of some species and life-stages, mostly affecting social interactions, as social interactions in small groups of fish usually lead to the formation of dominance hierarchies. Individuals within the same population are often differentially responsive to risk and use different tactics to compete for limited resources. In general, dominant fish can show more territoriality, holding better positions...
in the environment and better access to available food, being aggressive towards subordinate fish, which suffer behavioural inhibition, including reduced activity, feeding or mating.\textsuperscript{101,102,271} One of the main consequences of high concern for fish farmers is that these social hierarchies can lead to a high inter-individual growth variability, and even increase mortality within the rearing system, suggested as an adaptive strategy to optimise survival of the population in a restricted space.\textsuperscript{273}

Social interactions are also influenced by the physiological and behavioural differences in stress responses of each individual within a population or rearing unit, namely stress coping styles or personalities, which can have relevant consequences for aquaculture.\textsuperscript{274} In addition, several studies have demonstrated the ability of diverse farmed fish to recognise familiar conspecifics and consequent positive effects on social interactions.\textsuperscript{29,146,275} Familiarity stabilises the hierarchical structure of a group, and governs behavioural modifications (e.g., agonistic behaviours) that promote feeding and growth, leading to higher fitness and survival.\textsuperscript{29,275} Therefore, besides being affected by densities in relation to space, food distribution and food quantity, social interactions are also affected by familiarity and personality, and all these factors might be modulated through social enrichment, but also through feeding strategies (see dietary enrichment, section 2.5). Moreover, it is also important to consider that in farm conditions, it is possible to find more than one species in the same rearing unit, with some associated effects for welfare. For example, cleaner-fish such as lumpfish and diverse wrasse species are reared in net-pens together with adult salmon to reduce their parasitic load by feeding on the salmon lice copepod,\textsuperscript{103} although recent evidence highlights the questions on welfare and sustainability benefits of such practices, especially for the lumpfish and wrasse themselves.\textsuperscript{276} Noble et al.\textsuperscript{277} reported that growth performance and welfare of white-spotted charr (\textit{Salvelinus leucomaenis}), which are poor self-feeders, may be improved by growing them in tandem with experienced and proficient self-feeding rainbow trout. Recently, Thomas et al.\textsuperscript{278} showed positive effects on growth parameters and behavioural changes of juvenile zander (\textit{Sander lucioperca}) cultured in recirculating systems (RAS) with other species, such as sterlet (\textit{Acipenser ruthenus}) or tench (\textit{Tinca tinca}). Another example of co-existing different species, and therefore another kind of social enrichment strategy, is the polyculture in Asian and African ponds, where mainly several species of carps (e.g., \textit{Hypophthalmichthys molitrix}, \textit{Aristichthys nobilis}, \textit{Cyprinus spp.}) are reared together given their compatible spatial-trophic habits.\textsuperscript{279} In addition, diverse fish species can also be reared together in extensive and semi-intensive earthen ponds in estuarine areas of Southern Europe, such as European eel (\textit{Anguilla anguila}), grey mullet (\textit{Liza spp.}) or flatfishes (\textit{Solea spp.}), which already co-exist in natural conditions.\textsuperscript{280,281}

Finally, Fife-Cook and Franks\textsuperscript{206} recently suggested the possibility of directed fish-human interaction. According to these authors, this kind of inter-specific interaction may be motivated by curiosity, presenting an opportunity to explore and exercise agency, which could serve as a source of cognitive stimulation for some species of captive fish. However, before considering fish-human interaction as social enrichment, further work is still needed to explore this possibility.

### 2.5 Dietary enrichment

The last, but not the least, strategy to enrich the environment and thus the lives of captive fish is related to their diet. Dietary enrichment refers to the food type or feeding strategy (distribution, quantity, periodicity, etc.) which mostly affects foraging behaviour or food intake, but it does not include the composition of the diet (which would be considered “internal or nutritional” enrichment). Feeding strategies play an important role here as dietary enrichment, given that feeding regimens, schedules and procedures can highly affect, positively or negatively, fish welfare status.\textsuperscript{1,282} An appropriate feeding strategy adjusted to the biological needs of each species and life-stage can help control foraging behaviour and reduce undesired behavioural responses and social interactions. However, foraging behaviour is one of the widest and most complex areas of investigation, and it is difficult to develop a universal feeding strategy.\textsuperscript{283} Many species-specific factors are involved in the feeding strategies and tactics of fish, such as feeding rhythms, food ratio and feeding time.

In general, a self-feeding system improves fish welfare, allowing fish to choose their optimal feeding time and food ratio.\textsuperscript{283} However, automatic feeders can be used to deliver small quantities of feed at short intervals, whereas hand feeding allows better observation of fish reaction to the feed and reduces feed wastage, although increasing the labour demand. Farmers can also use feed spreaders that facilitate a more uniform and automatic distribution of feed throughout the rearing unit.\textsuperscript{284,285} It is noteworthy that a combination of feeding strategies appears most appropriate, but the observation of fish feeding response is essential and allows a quick adjustment of feeding strategies and diets, as well as a reduction of feed waste. Therefore, fish hunger and food availability are the main factors affecting fish welfare and effective production.\textsuperscript{282,286} A proper food availability consists on adequate distribution of food in time and space, food ration size, and food particle characteristics.\textsuperscript{282} In addition, farmers can benefit from current innovative, rapid, and non-invasive technology, such as intelligent feeding control methods (i.e., mathematical models, acoustic methods, optical sensors, and computer vision), which have improved drastically in recent years\textsuperscript{287,288} and are moving aquaculture towards a precision farming activity.\textsuperscript{289,290} Nevertheless, the implementation of technological developments is not feasible in all aquaculture facilities, as the initial financial investment may be high.

On the other hand, the selection of the appropriate type of feed as an enrichment strategy is also important. Feeds can be formulated diets (pelleted/extruded) or live prey, such as those used in hatcheries or in extensive and polyculture aquaculture. Indeed, periphyton-based aquaculture in earthen ponds, which is considered physical EE (see section 2.1.3), can be considered also dietary EE, given that the structures provide well-oxygenated surfaces for
periphyton to grow on, and the periphyton serves as food for many cichlids and cyprinids in aquaculture.\textsuperscript{112} Regarding formulated diets, they can be of different sizes and shapes, flavours, enhancers, texture, palatability and colour.\textsuperscript{291} Feeds can be also formulated to sink or float depending on where the fish usually feed within the water column. Taste preference or evaluation of sensory quality of grasped food items is a well-developed sense in fish, consisting mainly of the gustatory system.\textsuperscript{292} Such preferences in fishes are widely known for the many carnivorous species of farming interest, but also for some herbivorous species, and such knowledge is highly relevant for the feeding behaviour and preferences of each farmed species, also considering its life-stage and rearing systems, in order to improve the welfare status of captive fish (see section 2.2.3). Feed manufacturers already consider all these characteristics, and fish farmers can follow the manufacturer’s suggestions, choosing and selecting those feeds that are best suited to their fish.

3 | ENVIRONMENTAL ENRICHMENT AT FARMS: GUIDELINES AND CONSIDERATIONS

This review presents compelling evidence that EE influences the biological functions of fish in captivity. Appropriate enrichment increases the biological relevance of the living environment and promotes good welfare, both through overall health improvements and increased resilience to stressors. This is, to our knowledge, the most complete collection of studies regarding the full spectrum of EE and its effects in farmed fish to date. Nevertheless, these effects often vary in direction and magnitude, and each species and life-stage needs special consideration with respect to its natural history and preferences. In order to apply appropriate EE strategies, a possible first approach could be to evaluate specific preferences\textsuperscript{293} for different environmental resources or characteristics. This allows us to better identify which resources or characteristics fish really want, which is in line with the idea that to improve animal welfare, we should pay more attention to the wants and needs of the animals.\textsuperscript{294,295} In addition, determining their motivation to access specific resources is a complementary strategy that tells us how much the animal wants such preferable resources,\textsuperscript{296} thus highlighting which of them are more important than others. Preference and motivation tests differ in their approach (e.g.\textsuperscript{102,242,293,297,298}) but they both present an integrative view of what resources fish want and how much they want it. It is also important to consider that some EE features may be actively avoided and may represent a behavioural barrier preventing fish to access specific areas of the environment.\textsuperscript{299} and thus should also be taken into account for welfare purposes. The implementation of EE based on preferences and avoidances of fish is challenging, because fish are known to have considerable individual variability of preference responses.\textsuperscript{298,300} However, determining group preferences or, at least, which characteristics are preferred or avoided by the majority can help to better plan and implement EE strategies for farmed fish. This determination of fish needs and wants may be best achieved by an ethological approach: by addressing the causes and functions of behaviour (known as Tinbergen’s 4 questions\textsuperscript{301}), fish farmers can identify EE opportunities with the best probability of resulting in relevant improvements for their animals.\textsuperscript{302} For example, benthic species should benefit from substrate enrichment, which should nevertheless be appropriate for the life-stage in size and type. Conversely, there may be little advantage in providing physical enrichment for pelagic species or life-stages; instead, these fish would benefit more from occupational enrichment under the form of currents, or sensory enrichment such as wall/substrate colour patterns. This nature-based approach towards EE departs from the assumption that domestication in fish is very recent,\textsuperscript{4,5,302,303} and therefore, farmed fish species have essentially the same fundamental needs as their wild counterparts. The biology of fish in the wild is also highly informative on their welfare state because farmers can, for example, compare the behaviour observed in their systems with the known behaviours in the natural environment and use those comparisons as indicators of welfare.\textsuperscript{304} This is a central message of this review: the implementation of EE should be based on scientific knowledge of the animal, adapt the methods to the species and life stage and use the biology in the wild as a guideline, yet having in consideration the technical limitations (and possibilities) of each rearing systems.

The effective implementation of EE strategies at a commercial scale is still incipient. This may have two main sets of reasons:

1. Apparent cacophony of results: Several studies showed contradictory, undesired or unexpected results, which in most cases may reflect the use of inadequate design (or materials) for each species, life-stage and rearing condition. The effects of structural enrichment (probably the most direct form of EE) have been shown to be inconsistent amongst species, and therefore enrichment techniques may need to be adapted according to species-specific considerations. It should be noted that the specific items used as enrichment features vary between and within studies\textsuperscript{23,24} and may be responsible for the differences found. Reporting fine-scale characteristics of items used as enrichment in studies may help to reveal these last factors.\textsuperscript{24} Natural environments cannot be exactly recreated in farming systems, so the objective when designing enrichment is to modify elements of the artificial environments in order to provide welfare benefits without compromising the biosecurity of the farms. Hygiene and biosecurity currently seem to be the main concerns regarding physical EE; some structures or objects may accumulate food particles and faeces, making cleaning and disinfection difficult and compromising fish health and overall welfare. It can also happen that the structures leak out potentially hazardous chemicals to the environment (e.g. PVC phthalates), or that their design is inadequate and causes physical or psychological disturbances or damage to the fish (e.g. small holes, cracks, protrusions, noise), increasing the risk of infection, stress or mortality. All these factors should be considered when planning EE, and contingency plans as well as corrective actions (e.g. increasing or modifying cleaning
routines, monitoring fish behaviour upon deployment of EE, quickness to respond to negative effects) must be considered. Another aspect to consider is that the introduction of new objects in the environment can cause negative mental states (“neophobia”) in some fish, or an increase of territoriality and aggressive/defensive attacks. 

In addition, the type and intensity of EE should take into consideration the ethology of the species, so that the method is adapted to the fish and not the other way around, 

as well as the allostatic effect of the enrichment measures: whilst too little (or inefficient) stimulation will not produce positive effects, too much (or wrong) stimulation will produce distress. 

For example, in the case of forced-swimming exercise, currents may differ in different areas of the tank, subjecting some fish to too much or too little exercise; and social enrichment can cause stress by densities being too high or too low. 

Potential synergistic effects of two or more types of enrichment or stimulus that can amplify, reduce or even eliminate one another should also be considered when implementing EE strategies for farmed fish. In this sense, it should be noted that many types of EE may have already been tested in many more species than is known but, due to publication bias, the existing knowledge may be limited to the few that produced clearly visible or short-term effects.

2. **Industry hesitation:** Existing fish farming methods are mostly designed on practical, functional, economic and ergonomic requirements. Consequently, operational protocols in fish farms have been built on efficiency standards for such systems. However, most systems and methods have been designed when the science behind fish welfare, and specifically EE, was still in its early days. The implementation of EE requires a transformation of existing methods and protocols, so there may be an understandable resistance to change by the industry stakeholders, especially in a case where the results of such transformation do not seem to be consistent (see previous point). Any transformation or implementation at industrial scale entails a considerable financial investment, including time and personnel, and final results must be reputational and economically profitable. Furthermore, the challenges to implement EE differ regarding the type of system; whilst in extensive and semi-intensive farming, the deployment of EE may be feasible without much disruption to operational protocols, in intensive or ultra-intensive systems any small change may require large transformations in the procedures and may impact a huge number of animals (both negatively or positively). Finally, enrichment protocols may be protected by corporate secrecy, or there may simply be lack of stimulation to disseminate and share knowledge publicly. The industry would greatly benefit from consistent, reliable studies at a commercial scale, since much of the information remains in pilot or laboratory scale. This is especially relevant when market environments are changing; in the case of certification schemes, major labels are moving towards welfare standards and new requirements. The Friend Of the Sea ® label, for example, now requires at least some form of EE for most of their certified farmed fish species. 

It would therefore be in the best interest of the sector to respond to these market requirements. Comparing with the poultry and pig farming industry, these sectors stand out for how long there has been a push towards more welfare-friendly practices, and how recent are the advances in welfare requirements, specifically in EE. This represents an opportunity of the fish farming sector to catch up with its terrestrial counterpart, learn from its path and gain traction. Regardless of the main driver for this change (ethical, reputational, economic) what should be noted is that fish welfare awareness is already at an advanced stage, especially in the EU, from campaigns and retailer bans to certification and legislation (e.g., ). It is therefore time for research and industry to join forces so that EE in fish effectively works for the benefit of all parts.

Overall, EE strategies show the same pattern; there is no single silver bullet to design a fit-for-all EE strategy in any category. Interventions should be carefully planned, always considering that each combination of species, life stage, size, and type of group, density, type of rearing methods, type of operation, and so on, renders a unique arrangement that must be taken into account when designing and implementing EE in a commercial setting. The implementation of EE is, therefore, a process that requires caution and validation at each step. Consequently, we propose a decision-making framework to assist the process of implementation of EE in aquaculture in order to obtain positive benefits for the fish and the company (Figure 1). The selection, design and development of each EE strategy must be nourished with relevant information on both the target fish and farming facilities from the outset. Each strategy must then be validated by following a series of steps aimed at obtaining the desired results, starting from experimental approaches and scaling up. Based on these results, a cost-benefit analysis must be performed, considering the potential rewards expected from the EE implementation but also the total costs associated with taking that action or strategy in place. Farming companies have production demands whilst simultaneously need to meet the regulators and market expectations, which can lead to conflicts between protection and production. Ideally, an appropriate EE strategy must provide benefits for the fish and the company, such as improving the health and welfare of the captive fish, increasing the growth performance and resistance to diseases, which increases the product quality, reduces associated economic costs, improves rearing standards and overall improves the ethics and public perception of the company. If desired results are obtained from these analyses, implementation will then proceed. However, a close long-term monitoring of the implemented strategy should be carried out in order to evaluate its effects and to be able to apply corrective measures if necessary. Indeed, the application of operational welfare indicators (OWIs) throughout this process, such as specific behaviours or physiological parameters, is highly recommended for a much more accurate and successful assessment of the selected EE strategy on fish welfare. In addition, the use of precision fish farming tools could provide a technological support for farmers to monitor OWIs and safely implement measures that have the potential to greatly
improve the lives of countless farmed individuals. In case of undesired results in any of the steps described above, modifications in the design and development of the strategy should be made, applying the experience gained so far. In addition, the possibility of making modifications to some of the characteristics of the aquaculture facilities so that these, together with the EE strategy, are adapted to the fish, should be also reconsidered.

4 | CONCLUDING REMARKS

This paper reviews the range of possibilities and strategies for EE to be applied to different species of commercial interest and farming systems, in order to guarantee or improve the welfare of captive fish. It is clear that EE can improve the well-being of fish in captivity, providing stimulation to help meet their behavioural, physiological and psychological needs, increasing resilience and consequently reducing factors that impair not only welfare but also production. However, the effects of different EE often vary in direction and magnitude, and highly depend on each species and life-stage needs, preferences and natural history, combined with the characteristics of the fish farming system. Based on scientific knowledge, we discuss the feasibility and potential applications of different EE strategies, considering challenges and benefits for the aquaculture sector. We also provide a decision-making framework to address the design, validation and application of EE at industrial scale. Nevertheless, the
evidence base on this topic is still growing, and as such there are knowledge gaps regarding how environmental conditions should be modified to achieve all of the desired fish welfare and commercial benefits. Therefore, there is a need for further research and knowledge on the context-specific effects of different enrichment strategies for as many species and farming systems as possible, but above all, to demonstrate on-farm the applicability and feasibility of these strategies at commercial scale.

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